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Número 16

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Phylogeny of the *Cercomacra nigricans* species group (Aves: Thamnophilidae) and the biogeographical importance of Pliocene-Pleistocene tectonic movements

José Maria Cardoso da Silva

30 de dezembro de 1992

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Notes on *Knipolegus franciscanus* Snethlage, 1928 (Aves: Tyrannidae), an endemism of central Brazilian dry forests

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ABSTRACT — *Knipolegus franciscanus* of central Brazilian tropical deciduous forests, traditionally considered a subspecies of *K. aterrimus* of the Andes, shows a number of morphological, ecological and distributional characters that indicate that it should be considered a full species. Data on new specimens and a discussion of the biology and conservation of *K. franciscanus* are presented. We propose the common English name "Brazilian Black-tyrant" for the species.

KEY WORDS: *Knipolegus franciscanus*, Tyrannidae, Brazilian Black Tyrant, Brazil, Caatinga, Cerrado, Tropical Dry Forest.

RESUMO — *Knipolegus franciscanus* das florestas decíduas do Brasil Central, tradicionalmente considerada como subespécie de K. aterrimus dos Andes, mostra diversas características morfológicas, ecológicas e de distribuição, que indicam que é melhor considerada como espécie independente. Apresentamos dados sobre novos espécimes, bem como sobre a biologia e a conservação de *K. franciscanus*. Propomos que seja conhecida pelo nome vulgar em inglês de "Brazilian Black-tyrant".

PALAVRAS-CHAVE: *Knipolegus franciscanus*, Tyrannidae, Brazil, Caatinga, Floresta Decídua Tropical.

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INTRODUCTION

Knipolegus franciscanus was originally described as a subspecies of *K. aterrimus* by Snethlage (1928), but was considered as a distinct species by Silva (1989). Until our work *K. franciscanus* was known from only seven specimens collected in the Rio São Francisco valley (Snethlage 1928, Pinto 1938). Here we present arguments to support Silva's hypothesis and report new information on the distribution, habitat, behavior, taxonomic status and conservation of this poorly known species.

DISTRIBUTION

K. franciscanus has been reported only from the Rio São Francisco Valley: Januária (15°25'S, 44°25'W) and Pirapora (17°20'S, 44°54'W), Minas Gerais; and Bom Jesus da Lapa (13°16'S, 43°23'W), Bahia (Snethlage 1928, Pinto 1938). We collected 7 additional specimens (2 ♂ and 5 ♀) at Iaciara (14°09'S, 46°37'S) Goiás and 4 specimens (3 ♂ and 1 ♀) at Itacarambi (15°08'S, 44°04'W), Minas Gerais. In addition, we found an additional male specimen at the Museu National do Rio de Janeiro (MNRJ), collected by Rudolph Pfrimer in the Serra Geral of Goiás (MNRJ 10283).

Our specimens from Iaciara confirm that *K. franciscanus* occurs in the Rio Paranã valley (not to be confused with the Rio Paraná of south-central South America), a region ecologically very similar to the Rio São Francisco valley. The Pfrimer specimen has, however, an imprecise locality, since Serra Geral is a designation used to denominate the whole of the large sedimentary plateau between the borders of the Brazilian states of Goiás and Tocantins, in the west, and Bahia and Minas Gerais, in the east. It is possible that *K. franciscanus* occurs (or occurred) on the Serra Geral plateau, a region dominated by cerrado vegetation (a habitat type where *K. franciscanus* has not yet been recorded, see below), in the small patches of deciduous forests registered there by Brasil (1989), but today completely destroyed by soybean plantations (Silva, pers. obs.). However, since R. Pfrimer collected in both the Rio São Francisco and Rio Paranã valleys, and many of his labels present gross mistakes (Silva 1989), it is better to await more data before accepting the Pfrimer record.

SPECIMEN DATA AND ECOLOGY

All specimens (11) that we collected had the iris red, maxilla black, mandible black (9) or black with pink base (2 ♂), tarsi black. The mass of the males (x = 18.2 g, SD = 1.4) was similar to that of females (x = 18.2 g, SD = 0.89).

The males collected at Itacarambi in October 1988 had testes larger (7 x 3, 6 x 3 and 7 x 4 mm) than those collected at Iaciara (2 x 1 and 1 x 1 mm) in July 1989. The only female collected at Itacarambi had a large ovary (10 x 6 mm) and ova (4 x 3 mm), while the females at Iaciara had small gonads. It is possible that, as in other tyrants in Brazilian tropical dry forests (Silva, pers. obs.), *K. franciscanus* reproduces between October and February, the normal southern hemisphere bird breeding season (Pinto 1953, Oniki & Willis 1983).

We have observed *K. franciscanus* only in deciduous dry forests on rich soils, generally derived from limestone rocks. This special type of habitat is found in patches of variable size scattered throughout the cerrado and caatinga biomes, principally in the Rio São Francisco and Rio Paranã valleys (Ratter *et al.* 1978, Silva 1989). These forests are approximately 25 m tall, and characteristic tree species include *Astronium urundeuva, Piptadenia macrocarpa, Cedrella fissilis, Chorisia* sp. and in some areas *Cavallinesia arborea* (Ratter *et al.* 1978).

K. franciscanus is a common species in this type of forest, both intact forest and disturbed. It can also occur in pastures adjacent to dry forests, always in small trees. It was found (n = 32) solitary (46.8%) or in pairs (53.2%). The principal foraging methods of the species were short sallies from a perch to catch insects in the air (34) or on the upper surface of a leaf (19). It was also observed (2) participating in a mixed-species flock over *Eciton burchelli* army-ant raids together with *Thamnophilus punctatus, Formicivora melanogaster, Nonnula rubecula* and *Monasa nigrifrons*. In these circumstances, *K. franciscanus* executed short sallies above the ant swarm to capture flying insects or made short hops on the ground or on fallen tree trunks. When the bird hopped, it rapidly lowered and raised the tail in a characteristic fashion.

The species was mostly silent. We registered only one male making a buzzy "trrhie-tseet" while following army ants, and a female make a long series "thrriiiee-thrriiiee-tseep-tseep" while perched over a tall tree in the middle of a pasture.

TAXONOMY

To evaluate the taxonomic status of *K. franciscanus*, we examined 101 individuals (Appendix 1) of all taxa until recently (Traylor 1978) considered as *K. aterrimus*: the peri-Andean subspecies (*heterogyna, anthracinus, aterrimus*) and *franciscanus*. The specimens are housed in the following institutions: American Museum of Natural History, Louisiana State University Museum of Natural Science, Museu Nacional do Rio de Janeiro and Museu Paraense Emílio Goeldi.

The plumage variation of the peri-Andean taxa has already been well described in the literature (Hellmayr 1925, 1927, Fjeldså & Krabbe 1990) and will not be repeated in all details again here. The males are little distinct among the four populations. They are black, slightly lighter below, with a distinct large white patch on most of the inner webs of the primaries. Fjeldså & Krabbe (1990: plate 45) recorded that the males of *aterrimus* and *anthracinus* have the bill blue-gray tipped with black, while in *heterogyna* the bill is whitish with black tip. If this is the true pattern, the males of *franciscanus* are quite different, and all males we collected had the bill completely black. The red iris in *franciscanus* also appears to be unique, as the iris is dark brown in the other populations.

The female plumage, however, is highly variable among the populations, in yet another example of heterogynism in Neotropical birds (Hellmayr 1929, Sick 1975). There are differences between the females of *franciscanus* and the peri-Andean forms in underparts coloration. The breast in *franciscanus* is dominated by feathers with a black median surrounded by pale cinnamon or white. The belly and under tail coverts are principally white. This pattern is different from the peri-Andean forms, which can have the whole of the underparts dominated by bright ochraceous (*aterrimus*), bright ochraceous with black or dusky-gray flammulations in the breast (*anthracinus*) or pale ochraceous with throat and breast flammulated with dusky-gray or black (*heterogyna*).

The main difference between *franciscanus* and the peri-Andean forms is in the rectrices. All females of the peri-Andean populations have a well-defined color pattern in the rectrices (see detailed description in Hellmayr 1925 and Fjeldså & Krabbe 1990), mixing black with cinnamon rufous (*aterrimus* and *anthracinus*) or cinnamon buff (*heterogyna*). In *franciscanus* there is no such pattern, and the rectrices are all black, except the outermost, which have a well-defined narrow white outer margin.

Measurements are not very useful in discriminating *franciscanus* from the peri-Andean subspecies (Table 1), but *franciscanus* has, in both sexes, the smallest mean tarsus length, and largest mean female wing length. In the peri-Andean populations (Table 1), *anthracinus*, the central population, has the smallest measurements in comparison with the northern and southern populations (*heterogyna* and *aterrimus*, respectively).

Table 1. Mensural data (in mm) for *Knipolegus* spp. (means in parentheses)

	wing	tail	bill	tarsus
K. a. heterogyna				
♂	85.5-90.0(87.1) n=5; sd=1.8	74.0-79.0(76.7) n=5; sd=2.1	21.0-21.5(21.1) n=4; sd=0.2	19.5-23.0(21.0) n=5; sd=1.2
♀	75.0-80.5(77.8) n=6; sd=1.7	69.0-79.5(72.1) n=6; sd=4.2	20.0-22.5(20.8) n=6; sd=1.0	18.5-21.0(20.6) n=6; sd=1.0
K. a. anthracinus				
♂	79.0-82.5(80.9) n=10; sd=1.1	71.5-76.5(74.9) n=10; sd=1.4	19.0-21.5(19.9) n=10; sd=0.7	20.0-24.5(22.5) n=10; sd=1.5
♀	69.0-79.0(72.8) n=9; sd=2.9	66.0-73.0(67.9) n=9; sd=3.4	19.0-21.0(19.7) n=9; sd=0.7	20.5-23.0(21.7) n=9; sd=0.8
K. a. aterrimus				
♂	82.0-93.5(88.8) n=33; sd=2.9	73.5-88.5(80.0) n=32; sd=2.7	18.0-21.5(20.2) n=32; sd=1.0	21.0-24.0(22.1) n=33; sd=1.0
♀	76.5-88.5(82.1) n=13; sd=3.2	72.0-78.0(74.5) n=12; sd=2.1	18.0-20.0(19.2) n=12; sd=0.6	20.0-23.5(21.6) n=12; sd=1.2
K. franciscanus				
♂	83.0-90.0(86.3) n=9; sd=1.8	74.0-80.5(76.4) n=9; sd=1.9	14.5-18.5(16.7) n=9; sd=1.4	16.5-20.5(18.7) n=9; sd=1.2
♀	79.0-85.5(81.4) n=7; sd=2.7	72.0-78.5(74.5) n=5; sd=2.6	15.0-18.5(17.1) n=7; sd=1.1	16.0-21.5(18.9) n=7; sd=1.7

There is a striking difference in the pattern of sexual dimorphism in size relations in *K. franciscanus* as compared to the peri-Andean forms. By using the formula: (average ♂ measurement - average ♀ measurement ÷ average ♂ measurement x 100), we arrived at the following values:

	wing	tail	bill	tarsus
heterogyna	10.7	5.9	1.4	1.9
anthracinus	10.0	9.3	1.0	3.5
aterrimus	7.5	6.8	4.9	2.2
franciscanus	5.6	2.5	-2.4	-1.0

K. franciscanus, in addition to having the smallest level of sexual dimorphism in wing and tail measurements in the complex, is the only form in which the females have bills and tarsi on average longer than those of males.

Based on the differences in plumage coloration, mensural sexual dimorphism and the large disjunction in distribution (Fig. 1), we propose that *Knipolegus franciscanus* be recognized as a distinct species. We propose the English common name of "Brazilian Black-tyrant" for the newly separated taxon.

CONSERVATION

The recognition of full species status (see Willis and Oniki 1982) for these central Brazilian populations fortifies arguments by conservationists for the establishment of biological reserves to guarantee the preservation of characteristic segments of the central Brazilian dry forest, one of Brazil's most endangered habitats. The combination of clearing for irrigated and dry-field agriculture and charcoal harvesting for Brazil's iron and steel industries has devastated the great majority of this habitat; these forces continued unchecked. There is little recognition in Brazil or outside the country of the importance of this habitat to the preservation of Brazilian biological diversity, in spite of the fact that Brazil's tropical dry forests support a number of endemic species of birds and other taxa. In addition to the Brazilian Black-tyrant, other birds endemic to the vegetation-type include *Pyrrhura pfrimeri*, *Lepidocolaptes albolineatus wagleri*, *Xiphocolaptes falcirostris*, *Phyllomyias reiseri* and *Phylloscartes roquettei*.

Figure 1. Distribution of *Knipolegus* spp. (o = *K. a. heterogyna*; ▲ = *K. a. anthracinus*; ▽ = *K. a. aterrimus*; ★ = *K. franciscanus*.)

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APPENDIX 1: Specimens Examined

Knipolegus franciscanus. **Brazil.** Bahia: Bom Jesus da Lapa (2 ♀, including the type). Minas Gerais: Januária (4 ♂), Itacarambi (3 ♂, 1 ♀). Goiás: Serra Geral (1 ♂?); Iaciara (2 ♂, 5 ♀).

K. aterrimus heterogyna. **Peru.** Cajamarca: Cajabamba (2 ♂, 2 ♀), Hacienda Limón (1 ♂ imm.). La Libertad: Chusgon (1 ♂, 4 ♀), Huaylallas (1 ♂). Huancavelica: Fazenda Chacas (1 ♀).

K. aterrimus anthracinus. **Peru.** Puno: Carabaya (1 ♂, 1 ♀), Oconeque (4 ♂, 1 ♀, 2 ?), Valcón (2 ♂), Chichihuaya (1 ♀), 2 km NE Sandía (1 ♀), Alma de Maruncunca (1 ♂). Cuzco: Machu Picchu (1 ♀), Torontoy (4 ♂, 2 ♀, 1 ?), San Miguel (1 ♂, 1 ♀, 2 ?).

K. aterrimus aterrimus. **Bolivia.** Santa Cruz: California (2 ♀), Valle Grande (1 ♀). Chuquisaca: Tarabuco (1 ♂), Caballero (1 ♀). Cochabamba: Vinto (5 ♂), Tujma (2 ♂, 1 ♀), Parotani (6 ♂, 1 ♀). Sucre: Pulqui Alto (2 ♂, 3 ♀), Rio Pilcomayo (1 ♂). Potosi: Rio Cachimayo (1 ♂, 1 ♀). La Paz: Murillo (1 ♂). **Argentina.** Catamarca: Tiambala (1 ♂). Santiago del Estero: Lavalle (3 ♂). Tucumán: Tucumán (2 ♂, 2 ♀), Tapia (2 ♂), La Criolla (1 ♂), Tafí de Valle (2 ♂), Colalao del Valle (1 ♂), Norco (1 ♂), Vipos (1 ♀). Salta: Cachí (1 ♂).

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Bird observations in the State of Piauí, Brazil

Fernando C. Novaes [1]

ABSTRACT — Results of an ornithological collecting and observation expedition to the Uruçuí-una Ecological Station, Piauí, Brazil in December 1980 are presented, including data on habitat, foraging position, and sociality. Six bird species are recorded for the state for the first time.

KEY WORDS: Birds, Ecology, Piauí, Brazil.

RESUMO — Apresentamos os resultados de uma expedição ornitológica de coleta e observações feita à Estação Ecológica de Uruçuí-una, Piauí, Brasil, em dezembro de 1980, incluindo dados sobre habitat, altura de forrageio e sociabilidade. Seis espécies de aves são registradas pela primeira para o Estado.

PALAVRAS-CHAVE: Aves, Ecologia, Piauí, Brasil.

INTRODUCTION

The ornithological literature regarding the state of Piauí, Brazil is very limited. Hellmayr (1929) summarized the ornithological explorations of the state, which were carried out by J. B. Spix and P. Martius in 1819, Ottmar Reiser in 1903, and H. E. Snethlage in 1924. Not included in Hellmayr's work is the material collected by E. Kaempfer in Piauí in 1926 and 1927 and deposited at the American Museum of Natural History in New York City (Naumburg 1935). Because of the very little ornithological work done in Piauí, especially recently, we accepted the invitation of the Department of Biology of the Federal University of Piauí to make a visit in 1980 to the then recently founded Uruçuí-una Ecological Station under the administration of the Special

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Secretary of the Environment (SEMA-Secretária Especial do Meio Ambiente, Brasília). The station is located between 08°37'S to 09°10'S and 44°55'W to 45°30'W in the municipality of Ribeiro Gonçalves, with an elevation between 300 and 400 m; the highest elevation is in the hills of Serra Grande. The area lies between the Rio Uruçuí-preto and the Rio das Pedras and encompasses 135,000 ha. Other small water courses drain the station.

The dominant vegetation is cerrado intermixed with caatinga, but other kinds of vegetation are found, such as dry scrub forest ("mata seca arbustiva"), low riverine scrub forest ("mata baixa ribeirinha") and swamp vegetation dominated by buriti palms ("buritizais", *Mauritia flexuosa*) scattered in wet places and surrounded by the dry scrub forest. Some people live inside the station and maintain plantations of maize, beans, rice and other crops in small areas.

We stayed at the station from 6 to 12 Dec 1980. This period corresponds to the end of the six-month dry season; it did not rain during our stay. Two bird records were made outside the boundaries of the station: *Streptoprogne biscutata* shot at Serra das Confusões, Municipality of Caracol by Lieutenant-Coronel Lesbão Soares on 7/8 Dec 1980 (skins deposited at the Museu Paraense Emílio Goeldi, Belém); and *Passer domesticus* observed singing at 05:00 in the crown of a large tree in front of the Sambaíba Hotel, Teresina on 4 Dec 1980.

We follow Meyer de Schauensee (1970) for the sequence of species.

Key for Species List

Habitats
Ce = Cerrado (dominant vegetation in the area, intermixed with caatinga)
Ms = Dry scrub forest, "*mata seca*" (scattered between the cerrado and buriti palm swamp vegetation)
Mb = Low riverine scrub forest, "*mata baixa*" (main vegetation along the borders of water courses)
Bu = Buriti palm swamp vegetation (scattered in wet places)
Op = Open space (includes roads and clearings for human habitation)
Av = Above vegetation

Foraging position
A = Ground (species that catch food on the ground)
B = 1-5 m above ground
C = 5-15 m above ground
D = Aerial (soaring above any type of vegetation)

Sociality
S = Solitary (here includes foraging as individuals, in pairs and small family groups)
P = Pairs (foraging in pairs and small family groups)
G = Gregarious (unispecific flocks)

List of Species

Species	Habitat	Foraging position	Sociality
Crypturellus undulatus	Ce,Mb	A	S
Crypturellus parvirostris	Ce	A	S
Rhynchotus rufescens	Ce	A	S
Nothura boraquira	Ce	A	S
Anhima cornuta	Bu	A	P
Cathartes aura	Av	D	S
Ictinia plumbea	Mb	B	P
Buteo magnirostris	Ce	C	S
Buteo nitidus	Av	B	S
Herpetotheres cachinnans	Ce	C	S
Milvago chimachima	Ce	C	S
Falco sparverius	Ce,Av	C	P
Cariama cristata	Ce	A	S
Actitis macularia	Op	A	S
Columbina talpacoti	Ce,Op	A	S
Scardafella squammata	Ce	A	G
Anodorhynchus hyacinthinus	Av	C	P
Aratinga cactorum	Ce	C	P
Aratinga aurea	Ce	C	G
Forpus xanthopterygius	Ce	C	G
Pionus maximiliani	Ce	C	P
Amazona sp.	Ce,Av	C	P
Piaya cayana	Mb	C	S
Crotophaga ani	Bu,Op	A,B	G
Tapera naevia	Ce	A,B	S
Nyctidromus albicollis	Op	A	S
Reinarda squamata	Ce,Av	D	G
Campylopterus largipennis	Ms	B	S
Eupetomena macroura	Ce,Ms	B	S
Amazilia sp.	Bu	B	S
Trogon curucui	Bu,Ms	C	S
Momotus momota	Mb	C	S
Galbula ruficauda	Ce	C	S
Nystalus maculatus	Ce	C	S
Chelidoptera tenebrosa	Ms	C	P
Ramphastos toco	Ce	C	S
Colaptes campestris	Ce,Bu	B,C	P
Chrysoptilus melanochloros	Ce	C	P

Dryocopus lineatus	Ce,Bu	B,C	S
Leuconerpes candidus	Ce	A,B,C	P
Dendrocolaptes platyrostris	Ce	B,C	S
Lepidocolaptes angustirostris	Ce	B,C	S
Thamnophilus torquatus	Ce	B	S
Herpsilochmus pileatus	Ce,Mb	B	S
Formicivora rufa	Ce	B	S
Pachyramphus polychopterus	Ms	C	S
Tityra cayana	Ms	C	S
Tityra semifasciata	Ms	C	P
Tyrannus melancholicus	Ce	C	S
Tyrannopis sulphurea	Ce	C	S
Empidononius varius	Ce	C	S
Myiodynastes maculatus	Ce	C	S
Myiarchus ferox	Ce	C	S
Myiarchus swainsoni	Ce	C	S
Hirundinea ferruginea	Ms	C	P
Tolmomyias sulphurescens	Ce	B,C	S
Euscarthmus meloryphus	Ce	B	P
Elaenia chiriquensis	Ce	C	S
Suiriri affinis	Ce	C	S
Phaeomyias murina	Ce	C	S
Progne chalybea	Av	D	S
Cyanocorax cristatellus	Ce	C	G
Thryothorus leucotis	Mb	B	S
Troglodytes aedon	Ce,Mb	B	S
Turdus leucomelas	Ms,Mb	A,B,C	S
Mimus saturninus	Ce	C	P
Polioptila plumbea	Ce	B	S
Cyclarhis gujanensis	Mb	B,C	S
Vireo olivaceus	Ms,Ce	C	S
Parula pitiayumi	Ce	B,C	S
Euphonia chlorotica	Ce	C	S
Tangara cayana	Ce	C	S
Ramphocelus carbo	Ce,Mb,Bu	A,B,C	P
Cypsnagra hirundinacea	Ce	B,C	S
Neothraupis fasciata	Ce	C	P
Saltator maximus	Mb	C	S
Saltator atricollis	Ce	B,C	G
Oryzoborus angolensis	Ce	B	S
Charitospiza eucosma	Ce	C	G
Zonotrichia capensis	Ce,Ms	A,B	S
Spinus magellanicus	Ce	B	S

MISCELLANEOUS NOTES

New state records

The following species are recorded for Piauí for the first time here: *Colaptes campestris, Tityra semifasciata, Tyrannopis sulphurea, Hirundinea ferruginea, Tangara cayana,* and *Saltator maximus.*

Specimens collected

Because the collections were made within a protected area, only one specimen was collected of each species. Most specimens had tiny gonads which made sex determination extremely difficult.

Forpus xanthopterygius ♀, *Pionus maximiliani* ♀, *Trogon curucui* ♂, *Momotus momota* ♂, *Galbula ruficauda* o?, *Nystalus maculatus* o?, *Ramphastos toco* ♂, *Colaptes campestris* ♀, *Lepidocolaptes angustirostris* o?, *Dendrocolaptes platyrostris* o?, *Thamnophilus torquatus* o?, *Herpsilochmus pileatus* o?, *Formicivora rufa* o?, *Tityra cayana* o?, *Myiarchus ferox* ♂, *Myiarchus swainsoni* o?, *Suiriri affinis* o?, *Tolmomyias suphurescens* o?, *Elaenia chiriquensis* o? (2 individuals), *Phaeomyias murina* o?, *Cyanocorax cristatellus* juv. o?, *Thryothorus leucotis* o?, *Turdus leucomelas* o?, *Polioptila plumea* ♂, *Parula pitiayumi* o?, *Euphonia chlorotica* o?, *Tangara cayana* o?, *Cypsnagra hirundinacea* juv. ♀, *Charitospiza eucosma* ♂, *Zonotrichia capensis* o?, *Oryzoborus angolensis* o?.

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Phylogeny of the *Cercomacra nigricans* species group (Aves: Thamnophilidae) and the biogeographical importance of Pliocene-Pleistocene tectonic movements

José Maria Cardoso da Silva [1]

ABSTRACT — A cladistic analysis of the *Cercomacra nigricans* species group (*C. nigricans, C. carbonaria, C. melanaria, C. manu* and *C. ferdinandi*) is presented. The most parsimonious cladogram supports that: (a) *C. cinerascens* is the sister-taxon of the *C. nigricans* species group; (b) *C. ferdinandi* is the sister-taxon of the *C. manu-melanaria* clade. The separation between *ferdinandi* and the *manu-melanaria* clade is correlated with Plio-Pleistocene tectonic movements in the central Brazilian Plateau. The implications of this recent tectonism on speciation of the Neotropical birds are discussed.

KEY WORDS: Birds, *Cercomacra*, Cerrado, Neotropical region, Biogeography, Speciation.

RESUMO — Uma análise cladística do grupo de espécies *Cercomacra nigricans* é apresentada. O cladograma mais parsimonioso indica o seguinte: (a) *C. cinerascens* é o grupo-irmão do restante de todo o grupo de espécies *C. nigricans*; (b) *C. ferdinandi* é o grupo-irmão da clade formada por *C. manu/melanaria*. A separação entre *ferdinandi* e o grupo *manu-melanaria* é correlacionada com movimentos tectônicos que ocorreram no Planalto Centro-brasileiro durante a transição Plio-Pleistoceno. As implicações desse tectonismo relativamente recente sobre a especiação de aves neotropicais são discutidas.

PALAVRAS-CHAVE: Aves, *Cercomacra*, Cerrado, Região Neotropical, Biogeografia, Especiação.

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INTRODUCTION

The genus *Cercomacra* consists of 10 species of Neotropical forest birds (Meyer de Schauensee 1982, Sibley & Monroe 1990). There are two monophyletic species groups (*tyrannina* group and *nigrescens* group) and one intermediate species, *C. cinerascens* (Fitzpatrick & Willard 1990). The *nigricans* species group has a peculiar circum-Amazonian distribution (Fig. 1) and includes five well-marked species: *nigricans, carbonaria, manu, melanaria* and *ferdinandi*. Fitzpatrick & Willard (1990), when describing *manu*, proposed that *manu* and *melanaria* are sister species and that *ferdinandi*, the central Brazilian species, is closer to *nigricans* and *carbonaria*, two northern South American species, than to the *manu-melanaria* clade.

Here, I present a cladistic analysis of the *Cercomacra nigricans* species group, the result of which is discordant with the hypothesis of Fitzpatrick & Willard. In addition, I propose that a node of the proposed cladogram is correlated with Pliocene-Pleistocene tectonic movements of the Central Brazilian Plateau.

METHODS

To determine the phylogeny, I employed cladistic methodology (Hennig 1969). I examined skins of all species of genus *Cercomacra*, except *manu*, in the following institutions: Museu Paraense Emílio Goeldi (MPEG), Museu Nacional do Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo (MZUSP) and Zoological Museum, University of Copenhagen (ZMUC). In addition, I also utilized the voice and plumage descriptions presented in Fitzpatrick & Willard (*op. cit.*). The characters were polarized using the outgroup methodology (Maddison *et al.* 1984), with all other *Cercomacra* species utilized as the out-group. I used HENNIG86 (version 1.5) to derive the most parsimonious cladogram (command ie*). Characters were analyzed as unordered (comando cc-.) and with equal weight.
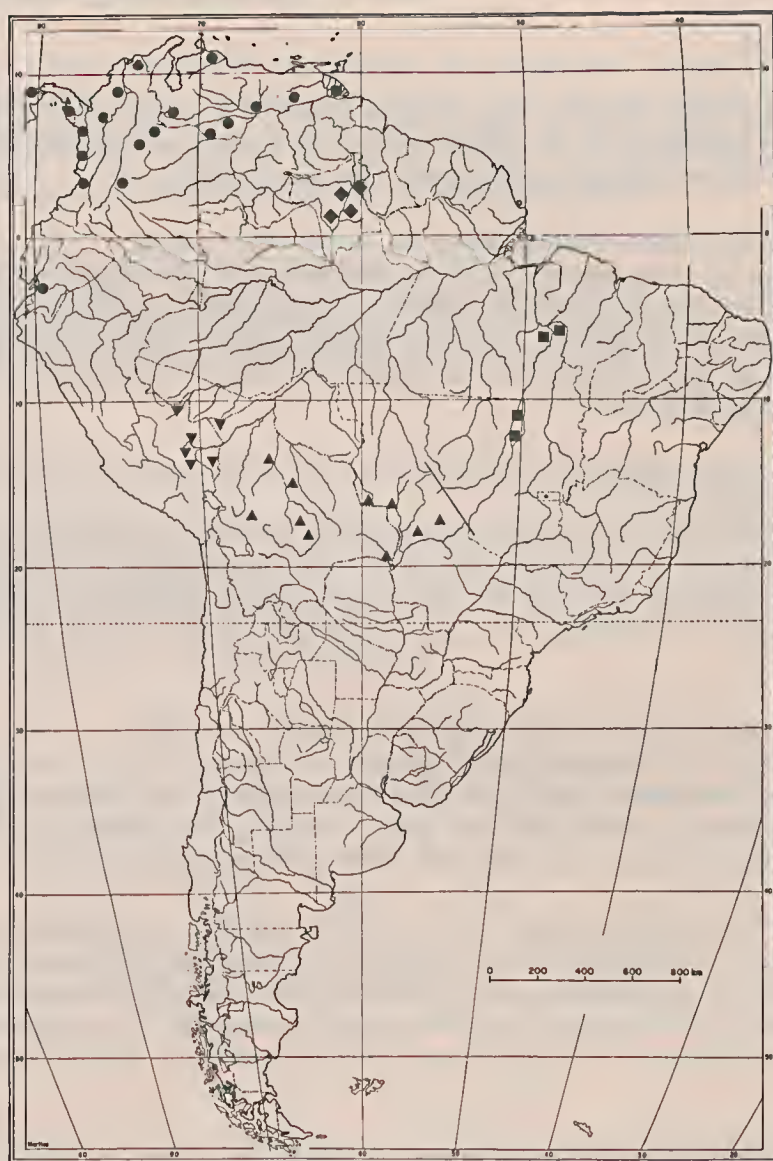
Figure 1. Distribution of the *Cercomacra nigricans* species group. (•) *nigricans*, (◆) *carbonaria*, (▾) *manu*, (▴) *melanaria* and (▪) *ferdinandi*. The line indicates the approximate location of the Guimarães Plateau.

RESULTS

I found seven characters that could be identified as apomorphic and that would be informative for the establishment of phylogenetic relationships within the *Cercomacra nigricans* species group. They are as follows:

(1) White-tipped rectrices (absent=0, narrow=1, broad=2).
All species of the *nigricans* group and *cinerascens* have white-tipped rectrices. There is, however, some variation within this group, since *manu-melanaria* have narrow white tips while the rest of the species have broad white tips. Both patterns are unique in the genus *Cercomacra* and they are interpreted here as derived character states.

(2) Primary vocalization dominated by a two-syllable component (absent=0, present=1).
In all members of the *nigricans* species group (Fitzpatrick & Willard op. cit.) and in *cinerascens* (Hilty & Brown 1986), the primary vocalization is dominated by a two-syllable component, "ker-chup". This sound is unique for *Cercomacra* (Fitzpatrick & Willard *op. cit.*) and is here interpreted as being a derived character.

(3) Male plumage predominantly black (absent=0 present=1).
Males of the *nigricans* species group are extremely similar, having the plumage predominantly black with white interscapular patches and white tips to all wing coverts and feathers at the bend of the wing. This plumage pattern is unique for the genus *Cercomacra* and is here proposed to be derived.

(4) Female throat streaked (absent=0, slightly marked=1, well marked=2).
Females of the *nigricans* species group have streaked throats (character state 2), although this character is less pronounced in *manu* (cf. description by Fitzpatrick & Willard op.cit.) and *melanaria* (character state 1). Both plumage patterns are unique in *Cercomacra* and are here interpreted as derived character states.

(5) Female belly gray (absent=0, washed with buff=1, dominated by gray=2).
Females of the *nigricans* species group have bellies gray (*nigricans, manu, melanaria,* and *ferdinandi*) or gray washed with buff (*carbonaria*). These color patterns are unique in *Cercomacra* and are interpreted here as derived character states.

(6) "Staccato whinny" notes (absent=0, present=1).
Fitzpatrick & Willard stated that only *manu, melanaria* and *ferdinandi* are known to have "staccato whinny" notes in their vocal repertoire. However, they

did not have vocalizations of *carbonaria* for comparision. I heard *carbonaria* vocalizations in the riverine forests near Boa Vista, Roraima, Brazil, in March 1990. I readily recognized a two-syllable component, but nothing that recalls "staccato whinny" notes. As the "staccato whinny" vocalization component is unique in *Cercomacra*, I interpret it as a derived character.

(7) Female breast black (absent=0, present=1).

The *nigricans* female has the breast strongly washed with black that sometimes extends to the abdomen. The other species of the *nigricans* group have breast varying from neutral gray (*melanaria*) to blackish gray (*ferdinandi*), but never black as in *nigricans*. This character is therefore interpreted here as derived.

I found two cladograms with a length of 11 steps, Consistency Index (CI) of 1.0 and Retention Index of 1.0. The best cladogram, that without any tricotomy, is presented in Figure 2. The cladogram supports that: (a) the *C. nigricans* species group is monophyletic, but could be expanded to include *C. cinerascens*, which is the sister-taxon of all other species of the group; (b) *C. ferdinandi* is the sister-species of the *manu-melanaria* clade.
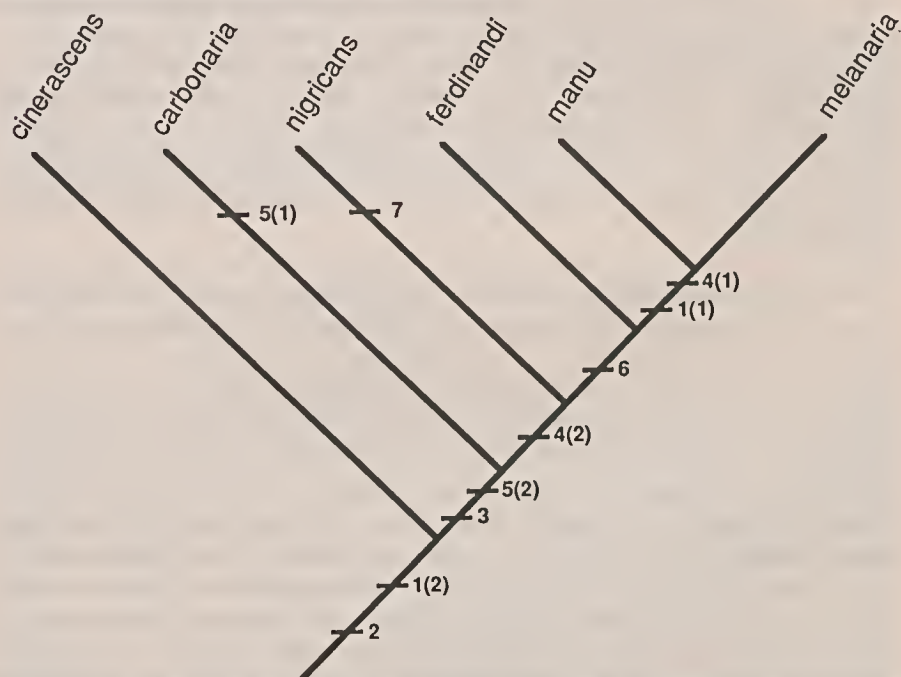
Figure 2. The most parsimonious cladogram of the relationships among the species of the *Cercomacra nigricans* species group. Character numbers according to text.

DISCUSSION

One could say that the cladogram presented (Fig. 2) has a limited heuristic value, due to small number of characters utilized. This is in fact a common problem with cladistic analysis at the species level in birds when only plumage and vocal characters are utilized. Christidis *et al.* (1988) and Hackett & Rosenberg (1990) have pointed out that in some situations cladograms generated by features of the external morphological are discordant with those generated by biochemical ones. However, phylogenetic hypotheses with good resolution power have been made utilizing only plumage and/or vocal characters (Haffer 1985; Cracraft 1986, 1988; Cracraft & Prum 1988).

The principal difference between my cladogram and the earlier Fitzpatrick & Willard hypothesis is the phylogenetic position of *ferdinandi*. I believe, however, that this discrepancy has two reasons: (a) the incorrect weight given by them to a plumage character (streaked throat), that was also considered as binary rather than as multistate; (b) the absence of the vocalization of *C. carbonaria* for comparision.

The cladogram presented here also makes sense biogeographically, since the distributional pattern of the *ferdinandi/manu-melanaria* clade (one species in the Araguaia River and the other in the Paraguay River system) is shared with at least one other monophyletic pair of bird species (*Synallaxis albilora-simoni*) which inhabits also the undergrowth of the riverine forests (pers. obs.). This pattern may suggest that these taxa also share a common history (Nelson & Platnick 1978). It is therefore useful to search for possible vicariant events that would explain it.

Fortunately, the geological history of the Guimarães Plateau is relatively well known. This moderately high tableland separates the Araguaia and Paraguay River drainage systems and as a consequence, the distribution of these bird clades (Fig.1). The plateau was covered by a fluviolacustrine system in the Pliocene, an interpretation supported by the presence of the Cachoeirinha Formation, a geological product of narrow continental sedimentation (Ross & Santos 1982). This paleo-environment could have had ecological conditions that allowed a continuous distribution of the ancestor species. After a leveling stage, this link between the two drainage systems was broken by an uplift followed by erosion that occurred in this region during the Pliocene-Pleistocene transition (Ross & Santos 1982). If this hypothesis is true, it could be expected that the distribution pattern shown by bird clades also may be shared with aquatic animals, more strongly associated with the river environments. Naércio A. Menezes (*in lit.*) has pointed out to me that the distribution pattern of sister-taxa occuring in Araguaia and Paraguay River systems is also found in fishes.

If the bird clade differentiation is associated with the geological event mentioned above, it is possible to estimate that the minimum age for the *C. manu/melanaria* clade, *C. ferdinandi*, *S. simoni*, and *S. albilora* is around 2 million years before present (ybp). This agrees very well with a recent estimate for species-level splits within some antbird lineages, utilizing genetic distances based on protein polymorphism (Hackett & Rosenberg 1990).

The predominant paradigm to explain species-level differentiation in the Neotropical avifauna is that based on the vegetational changes associated with cold-arid Cenozoic cycles (Haffer 1990). This model rests on the assumption that the extensive South American shield areas were stable land areas throughout most of the Cenozoic and consequently, faunal differentiation in these regions probably took place in the absence of conspicuous tectonic-geological vicariance events (Haffer 1985). However, this premise strongly contrasts with recent geological data that support extensive tectonic movements in these regions during the Plio-Pleistocene transition (see Petri & Fúlfaro 1986 for review). Studies on distribution and speciation of other species and subspecies in central and southeastern Brazil (Silva, unpublished data) support also the hypothesis that their origins are also associated with tectonic movements in the Plio-Pleistocene transition rather than with climatic-vegetational changes.

This information is congruent with Leon Croizat's early ideas (Croizat 1958, 1976) on bird speciation in the South America, since he strongly emphasized the importance of the tectonic movements and their results as the main vicariant events for interpreting species diversification in this continent. Croizat, however, perhaps based on the geological information at that time, assumed that these events had been older, at least middle Tertiary, than currently available information supports. Other students of Neotropical bird speciation have also suggested that some bird lineages were split due to tectonic movements during the Tertiary (Cracraft & Prum 1988).

I do not here wish to dismiss the importance of the Pleistocene-Holocene vegetational changes to explain the present patterns of bird distribution and perhaps populational differentiation, since they agree with the general knowledge about Quaternary climatic cycles (Haffer 1990). However, as has been pointed out for Neotropical forest butterflies, the species distribution patterns show no influence from refuges, but rather with the major physiographic barriers, resulting from Tertiary orogenies (Brown 1987). I feel that this is the pattern also in birds. It is, however, indispensible that future analyses of avian biogeography and speciation in the Neotropical region also consider the relatively recent tectonic movements and their influences (e.g., fluvial dynamics, subsidence terrains, etc.) in their interpretation rather than attempt to fit the data into a single pre-established model and accept for this a lot of unnecessary and unfounded assumptions.

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